Switching between Food Patches Suggests a Need to Balance Nutrients while Foraging in Wild Black Howler Monkeys (*Alouatta pigra*)

Nicoletta Righini[1,2*], Paul A. Garber[3], Jessica M. Rothman[4,5],
Minerva S. Santillán-Rivera[1,2], Antonio López-Espinoza[1,2]

[1]Universidad de Guadalajara, Centro Universitario del Sur,
Instituto de Investigaciones en Comportamiento Alimentario y Nutrición (IICAN),
Ciudad Guzmán, Jalisco, México

[2]Red Internacional de Investigación en Comportamiento Alimentario y Nutrición (RIICAN)

[3]Department of Anthropology and Program in Ecology, Evolution,
and Conservation Biology, University of Illinois, Urbana, IL, U.S.A

[4]New York Consortium in Evolutionary Primatology (NYCEP), New York, NY, U.S.A.

[5]Department of Anthropology, Hunter College of the City
University of New York, New York, NY, U.S.A.

Abstract

Studies of feeding patch choice in primates have traditionally analyzed individual foraging decisions in relation to patterns of social foraging, dominance, and feeding competition. However, information on detailed ecological and nutritional characteristics of the patches also is needed to understand the basis of feeding patch preferences. In particular, recent models of nutritional ecology have stressed the importance of nutrient balancing as a primary driver of individual foraging decisions. Here we investigated the behavioral and nutritional factors affecting feeding patch choice in black howler monkeys (*Alouatta pigra*) during a 15-month field study in Campeche, Mexico. We collected 1300 hours of behavioral data on 14 focal animals, including full-day follows of one individual/day recording all feeding activities. We carried out nutritional analyses of foods from feeding trees and calculated daily nutrient intake. A total of 690 trees (i.e., patches) were visited throughout the study period. The time spent feeding and the amount of food consumed differed significantly according to patch type. Individuals consumed more food in mature and immature fruit patches than in mature leaf, young leaf, and flower patches. Protein intake rates (kJoule/min) were similar in young and mature leaf patches, and higher than in mature fruit, immature fruit, and flower patches, among which the rate was similar. In the majority of the cases (80.3%), the focal animals left the feeding patch prior to satiation. On those occasions, resource mixing, or moving from one food type to another food type, accounted for 49.4% of the patch leaving events. The fact that black howler monkeys alternated feeding bouts between fruit and leaf patches, as well as alternating bouts of higher and lower protein intake, suggest that this pattern could be dictated by the need to balance nutrients.

Keywords: Feeding behavior; Food patch; Foraging; Mesoamerican primates'; Nutritional ecology

Resumen

Los estudios de elección de áreas de alimentación en primates tradicionalmente se han enfocado en analizar las decisiones de forrajeo en relación a patrones de forrajeo social, dominancia y competencia alimentaria. Sin embargo, para entender las bases de las preferencias de estas áreas se necesita también información sobre sus características ecológicas y nutricionales. En particular, modelos recientes de ecología nutricional han subrayado la importancia del balance nutricional como principal motor de las decisiones de forrajeo de los individuos. En este trabajo investigamos los factores que afectan la selección de las áreas de alimentación en monos aulladores negros (*Alouatta pigra*) durante un estudio de campo de 15 meses en Campeche, México. Colectamos 1300 horas de datos comportamentales de 14 animales focales, realizando seguimientos de un individuo por día, y registrando todas las actividades de alimentación. Llevamos a cabo análisis nutricionales de los alimentos colectados de los árboles de alimentación y calculamos la ingesta de nutrientes diaria. En el transcurso del estudio, fueron visitados 690 árboles (i.e., áreas). El tiempo de alimentación y la cantidad de alimentos consumidos difirieron significativamente de acuerdo al tipo de área. Los monos consumieron más alimento en árboles de frutos maduros e inmaduros que en árboles de hojas maduras, hojas jóvenes, y flores. Las tasas de ingestión de proteína (kJoule/min) fueron similares en árboles de hojas jóvenes y maduras,

---

* Corresponding author. Email address: nicoletta.righini@cusur.udg.mx

y más altas que en áreas de frutos y flores. En la mayoría de los casos (80.3%), los animales focales dejaron el área de alimentación antes de alcanzar la saciedad. En estas ocasiones, la mezcla de recursos (o sea la alternancia de las visitas a parches con diferentes recursos) explicó el 49.4% de los eventos de abandono del árbol. El hecho de que los monos aulladores negros hayan alternado eventos de alimentación entre áreas de frutos y hojas, así como entre ingestas de alta y baja proteína, sugiere que este patrón podría ser debido a la necesidad de balancear nutrientes.

Palabras clave: Áreas de alimentación; Comportamiento de alimentación; Ecología nutricional; Forrajeo; Primates mesoamericanos'

Introduction

Food items ingested by wild non-human primates usually occur in discrete food patches that can be monopolized by one or several group members (Isbell, 2012). However, the definition of a "food patch" can be challenging. Most field researchers studying arboreal primates have agreed to consider a patch as an aggregation of food items arranged in such a way that the forager can feed in it without interruption, and it can be represented by an isolated tree or a group of food trees of the same species with adjoining canopies (Leighton & Leighton, 1982; Chapman, 1988). However, it must also be considered that the forest canopy can be seen as a continuous environment, independent of the identity of individual trees, and using spatial analyses more in agreement with the forager's perspective would greatly improve the understanding of animal foraging decisions (Aristizabal et al., 2019).

The availability, distribution, and quality (e.g., size and density of food items) of feeding patches have an important effect on primate social organization, group cohesion, and feeding competition (Isbell, 1991; van Hooff & van Schaik, 1992; Peres, 1996; Koenig, 2000). Due to this, studies of patch choice have traditionally analyzed individual foraging decisions in relation to patterns of social foraging, spatial memory, dominance, partner preferences, and feeding competition (Garber, 2000; Di Bitetti & Janson, 2001; Kazahari & Agetsuma, 2008; Garber et al., 2009; King et al., 2009; Marshall et al., 2012; Kazahari et al., 2013; Tujague & Lahitte, 2013; Tujague et al., 2016). However, information on detailed ecological and nutritional characteristics of the patches is also needed to understand the basis of feeding patch preferences (Leighton, 1993; Marshall et al., 2012) and to shed light on the interaction between patch choice and social dynamics; for example, Busia et al. (2016) found that the size of subgroups a large community of spider monkeys (*Ateles geoffroyi*) in Mexico split into, was positively associated with the amount of protein in the feeding patches visited throughout the day.

Traditional ecological models based on Optimal Foraging Theory offer predictions to explain patch choice based on a "currency" (usually energy) that is expected to contribute significantly to fitness (Harrison, 1984; Stephens & Krebs, 1986; Ydenberg et al., 2007). Optimal Foraging Theory was modified by Charnov (1976) to include the Marginal Value Theorem (MVT), which predicts that foragers will remain in a food patch until the energetic intake

from that patch drops below the average value of other food patches in the environment. Once the current patch drops below this level, the forager is expected to search for another patch and feed there until resources in the new patch fall below the average patch value or the forager is satiated. In this model, a forager is expected to consider a patch to be functionally depleted prior to the time that all the food items are removed. In patches that minimally exceed the productivity of the average patch, changes in food density, resulting from the forager's feeding activity or the feeding behavior of other foragers, are expected to lower the patch value relative to non-exploited patches (Chapman & Chapman, 2000a). Thus, a patch can be considered functionally depleted when fewer suitable food items are left so that they are harder to find, or when all the items left, even if abundant, are not considered edible by the forager (e.g., unripe fruit, mature leaves).

However, more recent models of primate nutritional ecology have stressed the importance of nutrient balancing as a primary factor in individual foraging decisions (Felton et al. 2009a). Nutrient balancing is defined as a process in which decisions concerning where to feed and when to leave a patch are based on balancing the intake of protein, lipids, carbohydrates, minerals, and secondary compounds rather than maximizing the intake of energy or protein (Felton et al., 2009a). For example, a forager could leave a feeding patch before satiation or patch depletion and move to a different patch that contains complementary resources in order to ingest nutrients that will contribute to a more nutritionally balanced diet. Such a pattern has been reported in a variety of organisms ranging from invertebrates to primates (Houston et al., 2011; Simpson & Raubenheimer, 2012), and feeding trials with captive animals showed that foragers tend to choose "mixed diets" or feed to obtain particular macronutrient ratios even when foods that are considered preferred are offered *ad libitum* (e.g., tortoises (*Kinixys spekii*), Hailey et al., 1998; brown bears (*Ursus arctos*), Erlenbach et al., 2014; dogs, Roberts et al., 2018). Studies that have applied this framework to the analysis of feeding patch preferences of foragers in the wild are scarce (Felton et al., 2009a,b,c). One of the few examples assessed if folivorous guereza monkeys (*Colobus guereza*) foraged in food patches according to a fixed amount strategy (i.e., they leave after having eaten a fixed amount of food), a fixed time strategy (i.e., they leave after a constant time in the patch), or a nutrient balancing strategy (Johnson et al., 2017). The authors found that

guerezas did not employ either of the first two strategies, instead they maintained a balanced intake of macronutrients while visiting different patches. Monkeys spent more time feeding in patches with a specific non-protein/protein ratio, and fed less frequently and for less time in patches that differed from this balance, independently of the nutritional characteristics of the single foods present in the patch (Johnson et al., 2017). Another study (Tombak et al., 2012) on the same primate species (*C. guereza*) also reported that time spent feeding in a patch was not affected by tree size (which gives an indication of food amount), or by subgroup size (associated with possible feeding competition). The authors also found that these primates did not deplete the feeding patches, thus moving to another tree possibly to seek nutrient balance or to avoid accumulation of toxins that might be present in some leaf species (Tombak et al., 2012).

Here we investigate the factors affecting feeding patch choice in black howler monkeys (*Alouatta pigra*) during a 15-month field study in Campeche, Mexico. First, we identified the most commonly visited feeding patches and determined whether time spent feeding in each patch correlated with the amount of food consumed. Then, we examined how factors such as patch depletion, satiation, resource mixing (i.e., switch from one food type another), and social factors affected howler monkeys' decisions concerning when to leave a patch. Finally, we examined whether protein intake in a patch could explain patch choice and patch leaving patterns. We used these data to test the following hypotheses: **1)** Considering the relatively small group sizes of *A. pigra* (5-15 individuals), and the fact that howler monkeys frequently feed on large trees bearing fruits and leaves (Chapman, 1988), we expect an individual to leave a feeding patch prior to depletion (we define patch depletion based on observations of any group member returning to feed in the same patch during the same day or over the course of the next two days); **2)** Considering that leaves may contain higher amounts of potentially harmful secondary metabolites than fruits, and that fruits and flowers may be patchily distributed in space and time (Milton, 1980), we expect that a howler exits leaf patches before satiation, but exploits fruit and flower patches more intensively until satiated (i.e., not engaging in another feeding bout for at least one hour); **3)** An unsatiated individual who has not been threatened or displaced by a conspecific will leave a patch before it is depleted in order to locate a new food type that offers a complementary set of nutrients (e.g., switch from young leaves to mature fruits, or from flowers to mature leaves); **4)** If frequent switching between feeding patches is a strategy to mix resources and balance nutrients, a howler monkey will move from a feeding patch characterized by high (above average patch value) protein intake (kJ/min) to a patch characterized by lower protein intake (below average patch value) and *vice versa*.

Methods

Study Site and Subjects

This study was carried out at El Tormento (18º36′44″N; 90º48′31″W), a 2100-ha semi-deciduous forested area owned by Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP) in Campeche, Mexico. The climate is hot and humid, with three seasons: a dry and hot season from February to May (~100 mm rain during four months, 28°C mean daily temperature), a rainy season from June to September (~900 mm rain during four months), and a colder season ("*nortes*") from October to January (~160 mm rain during four months, 22.8°C mean daily temperature).

Two neighboring groups of black howler monkeys (*A. pigra*) were followed during 15 months. Group M contained 10-12 individuals and group J contained 6-7 individuals. The monkeys were individually recognized through their facial features, scars, and broken digits, and ten individuals were darted and marked with color anklets prior to the start of the behavioral data collection. Groups M and J ranged in areas of 14.5 and 4.5 ha respectively, with an overlap of 1.3 ha.

This research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Primates, and was performed under SEMARNAT and University of Illinois IACUC (#10051 and 10062) permits.

Field Data Collection

Behavioral data

Data were collected on howler monkey activity budget, diet, feeding patch occupancy, and within and between-group social interactions, conducting all-day follows of one adult individual per day (focal animal). We gathered 1300 hours of behavioral data on 14 focal animals (ten males and four females) using two-minute instantaneous samples on focal animals (Martin & Bateson, 2007). The activities recorded instantaneously included: feeding (i.e., ingestion of food items), resting, traveling, and social interactions (vocalizations, howling bouts, aggression, play, sexual interactions, affiliative behavior such as grooming). However, when the focal animal started feeding, we temporarily switched to a method of continuous data collection, recording the duration (to the nearest second) of each feeding event and the quantity (number of items, parts of the item, or bites per minute), phenophase (i.e., young/mature leaf, immature/mature fruit, flower/inflorescence, other), and species of the items ingested. Then, we resumed the two-minute instantaneous data collection. All feeding trees (n = 690) were tagged, measured (diameter at breast height, DBH) and identified. Data on displacements and agonistic interactions were recorded both by instantaneous

focal animal sampling (% of activity budget) and *ad libitum* (rates/hour), together with the identity of participants.

Feeding patches

We defined a feeding patch as a single feeding tree visited by the focal animal. A feeding bout was recorded when the focal animal was observed to handle and ingest a food item of a particular phenophase. A feeding bout ended when the focal animal stopped feeding for at least 30 minutes or left the food patch. In more than 50% of the cases, a feeding bout corresponded to the time the focal animal spent exploiting one food type in a feeding patch, but there were a few exceptions: 1) cases in which the focal animal fed on two or more phenophases in a single patch (e.g., switched from young leaves to mature leaves on the same tree); 2) cases in which the focal animal stopped feeding on a phenophase, began resting or performing other activities, and then resumed feeding on the same phenophase in the original patch after >30 minutes. In both circumstances, we counted these as two separate feeding bouts in one feeding patch.

We assumed that the focal animal might leave a feeding patch for the following reasons: 1) patch depletion, 2) satiation, 3) resource mixing, 4) social factors (e.g., aggression). Patch depletion was excluded if the focal animal or any group member was observed returning to feed in the same patch during the same day or over the course of the next two days. Moreover, we collected phenological scores (estimating the percentage of the crown containing food items on a scale of 0 − 4 [0; 1: 1−25%; 2: 26−50%; 3: 51−75%; 4: 76−100%]), and assigned a score to each patch immediately after the focal animal ended the feeding bout. We considered an individual to be satiated if it did not engage in a feeding bout for a period of at least 1 hour after terminating its previous feeding bout. Resource mixing was scored when the focal animal switched from one phenophase to another (e.g., fruits to leaves, or leaves to flowers) during successive feeding bouts within a period of < 1 hour. Other factors that we could not account for, might be involved in the decisions concerning when to leave a patch, for example the accumulation of particular plant secondary metabolites. Social factors included intra-group aggression over food, intergroup encounters (and howling bouts), mating behavior such as copulations and mate guarding, and other affiliative behavior such as play. Overall, we analyzed a total of 1678 focal animal feeding bouts.

Plant sample collection

Food items were collected from feeding trees either on the same day or within two days of the observed feeding bout. More details on plant sample handling are described in Righini et al. (2017). Briefly, the plant items were transported to the field laboratory, where they were measured and weighed, and air dried at a constant weight in a dark area, or, in the case of fruits, cut into small slices and kept in a drying oven (<50ºC) until reaching a stable dry weight. All samples (n = 146) were then stored in paper bags and maintained dry with a silica desiccant until phytochemical analyses were performed.

Laboratory Analyses

Plant samples were analyzed in duplicate in the Nutritional Ecology Laboratory at Hunter College, City University of New York. The samples were ground using a Wiley® mill fitted with a 1-mm screen. Dry matter was calculated by drying the field-dried samples in an oven (105ºC) immediately before each analysis to remove atmospheric moisture (Rothman et al., 2012).

Total nitrogen (N) was determined via combustion according to AOAC (1995) with a Leco TruSpec Nitrogen Analyzer (Leco Corporation, St. Joseph, MI, USA). Crude protein (CP) was calculated by multiplying N by 6.25 (Rothman et al., 2012). To take into account nitrogen bound to fiber and secondary metabolites, we also estimated available protein (AP) (Rothman et al., 2008; Righini et al. 2017). Available protein is reported in energy units, calculated using the standard conversion factors of 17 kJ/g (Conklin-Brittain et al., 2006).

Data Analysis

Nutrient intake

A complete dietary profile for each adult group member was built by quantifying feeding rates and estimating daily nutrient and energy intake. In all analyses related to nutrient intake, we included 91 focal sample days of 9 males (n = 44) and 4 females (n = 47), which correspond to 91 observation days in which the focal animal could be successfully followed for a period of 9 − 12 consecutive hours without being out of sight for more than 10 minutes, and all feeding bouts engaged in by the focal animal were recorded in detail. To analyze the effect of protein intake on patch choice, we divided each of the 91 days of observation in two blocks of 5-6 hours each (morning and afternoon). In most cases, the end of the morning block coincided with the start of a long resting bout that lasted on average 3.7 (± 1.6) hours. This was done to determine whether protein intake earlier in the day influenced protein intake later in the day.

To calculate the daily amount of food ingested (g dry weight) by each focal animal, we multiplied the feeding bout length on food item *i* (minutes) by the corresponding feeding rate (g dry weight/min), and then summed all daily events. To estimate daily nutrient intake, we multiplied the nutrient content of each food item *i* by the estimated amount of item *i* ingested (g dry weight) in each feeding bout. In this way, we obtained daily values (converted to

kilojoule equivalents) of protein intake for each focal animal. To take into account the possible effects of different body weights on nutrient intake in male and female howler monkeys, we divided the amount of food consumed (grams dry weight) and nutrient intake by the metabolic body mass (mbm = $M^{0.762}$) of the corresponding focal animal. Body mass for nine of the 14 focal animals was obtained during the darting and marking phase (adult males: 7.6 ± 0.9 kg, adult females: 6 ± 0.3 kg). For those individuals whose weights were not available (n = 4), we used data on mean body weight of male and female *A. pigra* from Kelaita et al. (2011), since they were based on a larger sample size (37 males, 32 females).

Statistical analyses

To test for differences in the amount of food consumed, time spent feeding, and rate of protein intake in fruit, leaf, and flower patches, we used one-ways ANOVAs and Kruskal-Wallis tests, when the variables did not conform to normality and homoscedasticity assumptions. Spearman's rank order correlations were used to analyze the relationship between time spent feeding in a patch and amount of food ingested, and between morning and afternoon protein intake. We used chi-square tests to determine if the frequencies of switching between different patch types differed from expected values based on a random distribution.

We used Linear Mixed-Effect Models (LMM) (Zuur et al., 2009) to analyze 1) if the number of feeding patches visited in the afternoon (response variable) could be predicted by the number of feeding patches visited in the morning (fixed factor), and 2) if the afternoon protein intake (response variable) could be predicted by the morning protein intake, also taking into account 3) other predictor variables such as sex of the focal animal and season. All models included the identity of individuals as a random factor. Data were square root transformed to conform to assumptions of normality. Akaike's information criterion (AIC) scores were used to compare models. All the analyses were run in *STATISTICA 12* (StatSoft, Inc., 2011) and R version 3.5.0 (R Core Team, 2018), fitting the linear models by REML (Restricted Maximum Likelihood criterion), and using the *nlme* package (Pinheiro et al., 2019).

Results

Visited feeding patches

A total of 690 feeding patches were visited throughout the study period (1300 hours of observation). Sixteen percent of the feeding patches were visited on two of 145 observation days, not necessarily consecutive; 7.2% were visited on three observation days; 3% on four observation days; and 4.7% on 5-13 observation days. The most visited patch (on 13 days) was a single *Brosimum alicastrum*

(Moraceae) tree, in which the focal animals fed on mature and young leaves, immature fruits, and inflorescences across the three seasons. Overall, young leaf patches were the most visited (31.6% of the total number of visited feeding trees), followed by immature fruit (21.6%), mature leaf (19.3%), mature fruit (18.7%) and flower/inflorescence (8.2%) patches.

The time spent feeding per patch visit differed significantly according to the type of food consumed (Kruskal-Wallis; H = 143.1, df = 4, n = 1667, p<0.0001). Individuals spent on average more time feeding in flower (11.6 ± 12.8 min), mature (10 ± 11.7 min) and immature (8.9 ± 12.2 min) fruit patches than in young (5.2 ± 6.3 min) and mature (3.9 ± 4.9 min) leaf patches (Figure 1). In addition, the amount of food (in grams) consumed per feeding bout by the focal animals differed significantly according to the food type (Kruskal-Wallis; H = 106.6, df = 4, n = 1667, p <0.0001). On average, individuals consumed more food in mature (20.3 ± 33.1 g dry weight) and immature (20.6 ± 25.6 g) fruit patches than in mature leaf (11.9 ± 17.6 g), young leaf (10.9 ± 15.6 g), and flower/inflorescence (9.3 ± 10.5 g) patches (Figure 2). Time spent in a feeding patch and the amount of food ingested correlated positively (Spearman correlation, r = 0.83, n = 1665, p <0.001). However, while howler monkeys tended to feed on flowers/inflorescences for as much time as fruits (11.6 min vs. 9.5 min on average), the amount in grams of flowers ingested per feeding bout was significantly lower due to their low dry weight (9.3 g vs. 20.5 g on average).

Leaving a feeding patch

Despite the fact that the majority of the feeding trees were not re-visited by the focal animal within two days of the initial feeding bouts, the same feeding patch was visited more than once during the same day on 53% of the 145 observation days, and we only recorded four instances of patch depletion. Each of these occurred in flower patches (i.e., there were no flowers left in the patch after the feeding bout). In more than 80% of the cases, the phenological score (0-4) recorded at the beginning and at the end of the feeding bout did not show a decrease (i.e., reduced by at least a factor of two). Moreover, time spent feeding in a patch (mean: 7.28 min) was not influenced by patch size (mean DBH: 41.6 cm) (Figure 3). Thus, overall, patch depletion was unlikely to explain the majority of cases in which the howlers left a feeding patch.

We recorded evidence of satiation in 19.6% of the cases: of these, 20.4% of the time the forager appeared satiated after feeding in a fruit patch, 17.3% after feeding in a leaf patch, and 10.9% after a feeding bout in a flower patch. These values are standardized according to the total number of fruit, leaf, and flower patches visited. Despite the fact that, as hypothesized, satiation was more frequently associated with fruit patches, these results did not differ from what

Figure 1
Time spent feeding (minutes) in different types of feeding patches. Medians, 25%-75% confidence intervals, non-outlier range, and outliers are shown. FL, flowers and inflorescences; ML, mature leaves; YL, young leaves; IF, immature fruits; MF, mature fruits.
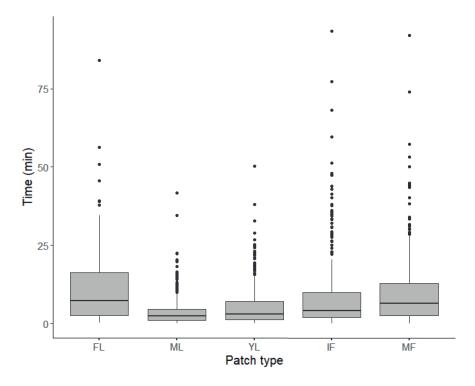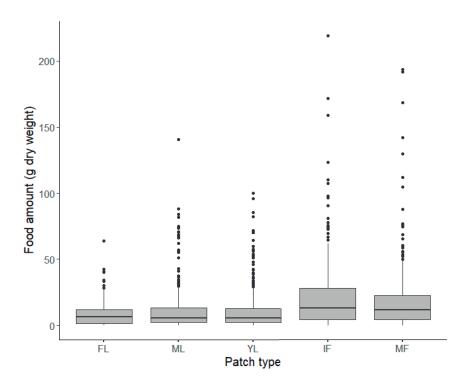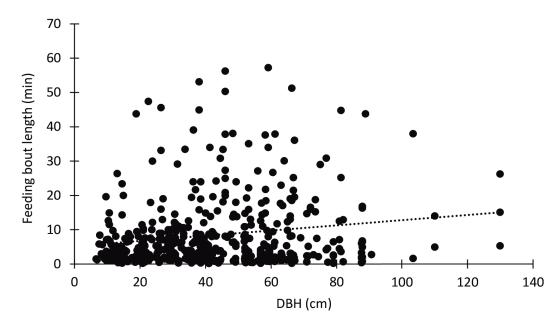

Figure 2
Amount of food (grams dry weight) consumed in different types of feeding patches. Medians, 25%-75% confidence intervals, non-outlier range, and outliers are shown. FL, flowers and inflorescences; ML, mature leaves; YL, young leaves; IF, immature fruits; MF, mature fruits.

expected based on an equal distribution of satiation among patch types (Chi-square test: $\chi^2 = 2.85$, df = 2, p = 0.23).

In the majority of the cases (80.3%), the focal animal left the feeding patch prior to satiation. On those occasions, resource mixing, or moving from one food type to another food type, accounted for 49.4% of the patch leaving events. The most frequent observations (Figure 4) included switching from a young leaf to an immature fruit patch (12.5%), switching from feeding on mature fruits to young leaves (12.2%) and from immature fruits to young leaves (12.2%). These values differed significantly from the frequencies expected if switching between patch types was based on no preference ($\chi^2 = 6.40$, df = 1, p <0.02; $\chi^2 = 5.75$, df = 1, p <0.05, respectively). In contrast, switching from mature fruits to flowers was observed significantly less than expected ($\chi^2 = 4.10$, df = 1, p <0.05). These data support the hypothesis that howler monkeys frequently alternate between food patches to consume different plant parts, in particular frequently switching from fruits to young leaves.

Finally, social factors (n = 100) accounted for only 8.1% of patch leaving events. In these cases, intergroup encounters (in the form of howling bouts or chases) were the most common social factor (53%, n = 53) that resulted in leaving a patch, followed by feeding related intra-group aggression (24%), mating behavior (e.g., copulation, mate guarding) (19%), and other reasons (e.g., play) (4%). Overall, contest feeding competition occurred at a rate of 0.018 events/hr (24 aggressive interactions across 1300 hours of observation), or 0.0019 events/min (considering total feeding time, i.e., 200 hr), and therefore appeared to play a minimal role in howler patch choice. Moreover, these intra-group direct aggression or overt displacement events were not asso-

ciated with a specific type of food patch; nine occurred in young leaf patches, six during immature fruit consumption, four during mature leaf eating bouts, three in mature fruit patches, and two while feeding on inflorescences.
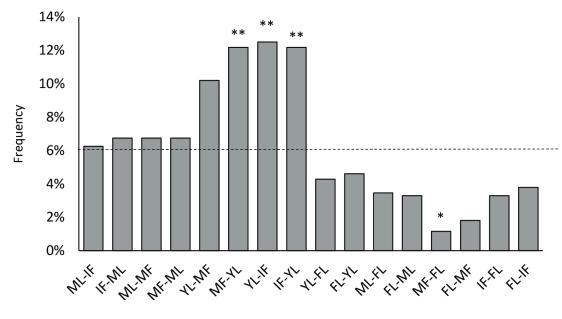
Patch choice from a nutritional perspective

The average number (±SD) of feeding bouts per day was 14.0 (± 5.01); 7.3 (± 3.5) in the morning and 6.7 (± 3.5) in the afternoon (Table 1). On average, the howlers fed on a similar number of trees in each time block (One-way ANOVA; $F_{(1,180)} = 1.3$, p = 0.25), but the number of patches visited in the afternoon was not predicted by the number of patches visited in the morning (LMM; estimate = -0.005, standard error = 0.10, t = -0.05, df = 77, p = 0.95). Moreover, the number of patches visited in the morning did not have a significant effect on the amount of protein ingested in the morning (LMM; estimate = 0.22, standard error = 0.33, t = 0.68, df = 77, p = 0.49) or in the afternoon (LMM; estimate = -0.27, standard error = 0.36, t = -0.75, df = 76, p = 0.45). However, the number of feeding patches visited in the afternoon did affect positively afternoon protein intake (LMM; estimate = 1.20, standard error = 0.34, t = 3.45, df = 77, p <0.0001), indicating a change in howler behavior such that higher intakes were achieved by visiting a greater number of feeding patches.

The rate of protein intake (kJoule/min) was similar in young and mature leaf patches (Kruskal-Wallis, H = 368.2, n = 1352, p = 0.9), and higher (p <0.0001) than protein intake in mature fruit, immature fruit, and flower patches (which, instead, had similar rates, p = 0.9) (Table 2). This pattern was consistent in the morning and in the afternoon.

Figure 4
Resource mixing by black howler monkeys. Frequency of switching from one feeding patch type to a different patch type. Frequencies are calculated taking into account the total number of patch-switching events. The dashed line shows the expected frequency of switching between patch types based on the total number of events and no preference. Asterisks represent significant differences from the expected values (** $p<0.02$; * $p<0.05$). Feeding patches: ML, mature leaves; YL, young leaves; MF, mature fruits; IF, immature fruits; FL, flowers and inflorescences.

The data also indicate that total protein intake during the afternoon feeding bouts was significantly predicted by the protein intake in the morning (LMM; estimate = 0.28, standard error = 0.11, t = 2.55, df = 77, p = 0.012). According to Akaike´s Information Criterion (AIC), the model including also the sex of the focal animal and season as predictor variables (AIC = 414.09) could be considered equally appropriate as the model with only protein intake (AIC = 414.7). However, the sex of the focal animal (LMM; estimate = -0.82, standard error = 0.47, t = -1.73, df = 11, p = 0.11) and season (LMM; *Nortes*, estimate = 0.80, standard error = 0.53, t = -1.33, df = 75, p = 0.18; Rainy, estimate = 0.44, standard error = 0.60, t = 0.82, df = 75, p = 0.41) did not have significant effects on temporal patterns of protein intake. Figure 5 shows the positive correlation between protein ingested in the morning and protein ingested in the afternoon. Thus, a higher cumulative intake of protein in the morning was followed by a higher intake in the afternoon. Likewise, mornings characterized by a lower than average nutrient intake, were followed by a similar cumulative nutrient intake in the afternoon. This is also shown by the fact that patterns of protein intake were extremely similar during the two temporal blocks (morning and afternoon) (Table 1).

Table 1
Daily protein intake by focal individuals and characteristics of feeding bouts during two temporal blocks (morning and afternoon) (n = 91 observation days). SD = standard deviation.

	Number of feeding patches visited	Food amount consumed (g dry weight/ mbm)	Protein (kJ/ mbm)
Morning			
mean	7.32	27.57	53.95
SD	3.52	15.43	33.91
Afternoon			
mean	6.75	25.16	48.33
SD	3.52	14.79	33.08

Figure 5
Positive correlation between protein intake during the morning bouts and protein intake during the afternoon bouts (protein values in kJoule per metabolic body mass are square root transformed).
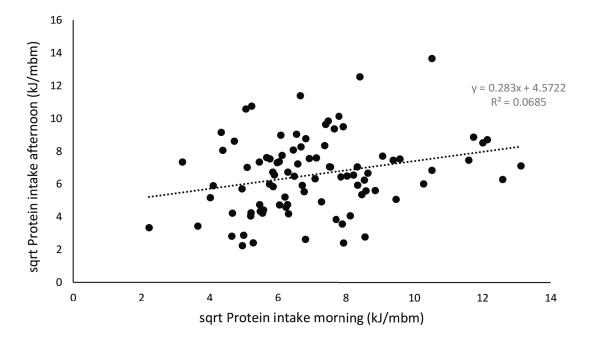

Table 2
Individual rates of protein intake (kJ/min) in different types of feeding patches during the morning and afternoon (n = 91 observation days). Feeding patches: ML, mature leaves; YL, young leaves; MF, mature fruits; IF, immature fruits; FL, flowers and inflorescences.

	Morning					Afternoon				
	n	Mean	Min	Max	SD	n	Mean	Min	Max	SD
FL	76	2.17	0.19	10.56	1.88	46	3.44	0.14	10.83	3.11
MF	118	2.77	0.30	11.72	2.15	121	2.71	0.59	11.72	1.78
IF	172	2.25	0.13	10.09	1.80	143	2.70	0.50	11.72	2.24
ML	96	6.71	1.42	23.02	4.90	124	5.89	0.61	18.62	4.53
YL	249	4.99	0.86	17.25	2.84	207	5.06	0.44	23.03	3.01

Discussion

Studies of feeding patch choice offer insights into the mechanisms used by individuals to decide which patch to visit, when to leave a patch, and which patch to visit next. These decisions are affected by patterns of food distribution and availability, within-group and inter-group feeding competition, and nutrient needs (Stephens et al., 2007). In this analysis of the feeding patch choices of black howler monkeys, we found that howlers rarely depleted a food patch prior to leaving. Similarly, howlers left a patch in response to satiation only 19.6% of the time. However, instances of satiation were more frequent during fruit feeding than in leaf patches, but the difference was not significant.

Thus, it appears that, according to our definitions, neither satiation nor patch depletion explained the majority of patch choice decisions made by howlers. In addition, we recorded few instances of social interactions during feeding, and aggression over food occurred at very low rates (only 24 aggressive interactions were recorded across 1300 hours of observation of 14 focal animals), indicating that within group contest competition was not a significant factor primarily affecting individual foraging decisions, similarly to what as has been reported in other howler monkey populations (Wang & Milton, 2003; Garber & Kowalewski, 2011). Instead, the data presented here support a resource mixing strategy, with howlers frequently leaving an undepleted patch of a particular food type to move to another

patch containing a complementary food type. In particular, howlers frequently switched between young leaves and immature fruits, mature fruits and young leaves, and immature fruits and young leaves during successive feeding bouts. These resources differ in nutritional content, with young and mature leaves being higher in available protein (~13.4% dry weight) and neutral detergent fiber (48.8%) than mature fruits (7.5% and 33.6%, respectively), and mature fruits having a higher lipid (11.1%) and sugar (23.6%) content than leaves (2.19% and 5.5%, respectively) (Righini et al., 2017). Protein intake rate was significantly higher in leaf patches than in fruit patches, and the most common pattern observed in howlers across successive feeding patches was to move from a lower protein patch to a higher protein patch, and from a higher protein patch to a lower protein patch. However, despite these fluctuations in protein intake from one patch to the other, the cumulative amount of protein obtained in the afternoon was positively affected by the cumulative amount ingested in the morning, indicating that howler monkeys maintained a specific daily intake strategy that allowed them to achieve a targeted proportion of nutrients.

Do black howler monkeys leave a feeding patch due to patch depletion?

Models of optimal foraging generally assume that foragers deplete (or functionally deplete) a patch prior to leaving it. In primates, this has been examined in the context of within-group feeding competition (Snaith & Chapman, 2005, 2008). In the case of scramble or indirect feeding competition, access to food resources is generally unaffected by rank or aggression. Rather, the first individual to arrive in a patch may obtain a finder's advantage and consume all the foods in the patch, especially in food patches characterized by small, concentrated food items such as ripe fruit (Janson & van Schaik, 1988; Bicca-Marques & Garber, 2005; Garber et al., 2009). It also has been argued that, in small food patches, foraging efficiency of lower ranking individuals declines with increasing group size, as a limited number of high ranking individuals can deplete the patch. Under these conditions, aggression at feeding sites is expected to be high and foragers are expected to switch frequently between patches and travel greater distances to encounter a larger number of food patches (Janson & van Schaik, 1988). These assumptions, which are part of the ecological constraints model (Chapman & Chapman, 2000a,b), also imply that most food patches encountered by wild primates are depletable, which is not always the case. Despite the fact that this model was initially presented to explain patterns of subgrouping and patch choice in frugivorous primates, it has been extended to explain the socioecology of leaf-eating primates (Snaith & Chapman, 2005, 2007, 2008). For example, whereas red colobus monkeys (*Procolobus rufomitratus*), living in groups of up to 18 individuals, depleted patches of young leaves (Snaith

& Chapman, 2005), groups of sympatric guerezas (*Colobus guereza*), ranging in size from 4 to 11 individuals, did not appear to deplete feeding patches, based on the fact that time spent feeding in a patch was not a function of either patch size or feeding party size (Tombak et al., 2012).

In the present study of black howler monkeys, within group contest competition at feeding sites was very low. Moreover, time spent feeding in a patch was not a function of patch size (i.e., tree DBH), and in over 80% of the cases, howlers left a feeding patch before depletion. Similar results were found for *Alouatta caraya* in Argentina, where several neighboring groups were observed feeding in the same trees during consecutive days; the same feeding tree was revisited on the same day during 36-65% of days; and within-group aggression at feeding sites was very low (0.002-0.004 agonistic interactions per individual per hour) (Kowalewski, 2007). Additionally, neither patch size, nor the number of individuals in the feeding party had an effect on time spent feeding in a patch (Kowalewski, 2007). These patterns differed from those reported in a study of *A. palliata* in Costa Rica (Chapman, 1988). When mantled howlers fed in fruit patches, patch size and the number of individuals in the subgroup were positive predictors of time spent feeding. These interspecific differences in foraging strategies and patch use might be analogous to those found in colobines, especially considering that group size in *A. palliata* is much larger than in *A. pigra* and *A. caraya* (for example, the group studied by Chapman [1988] consisted of 40 individuals).

At our study site we only recorded four cases of patch depletion in flower patches. Flowers are an ephemeral resource that is not available throughout the year. The flowers consumed by our study groups were relatively rich in available protein (>15% dry matter) and carbohydrates (TNC >55%), and contained relatively low concentrations of indigestible fiber (ADF ~ 14%), thus they seemed to be a preferred resource when they were available (Righini et al., 2017). It was common that howler monkeys stayed in flower patches longer than in other patch types, but due to the flowers' low dry weight and low feeding rates (1.00 ± 0.6 g/min vs 3.45 ±1.9 g/min for mature leaves), the amounts of total dry matter ingested after a feeding bout were not conspicuous.

Do black howler monkeys leave a feeding patch due to satiation?

According to Optimal Foraging Theory and the Marginal Value Theorem, food intake rates decline as time spent feeding in a patch increases (Charnov, 1976; Stephens & Krebs, 1986). However, two different factors affect feeding rates. Declining feeding rates could indicate both patch depletion (or declining abundance of food resources) and/or forager satiation (Grether et al., 1992). Tombak et al. (2012) reported that, in the case of guerezas, individuals left feeding patches most likely due to satiation rather than

to patch depletion because they maintained a constant feeding rate (bites/min) without an increase in movements within the patch, which was assumed to be a measure of feeding effort. A study modeling foraging preferences and analyzing the decision rules of three groups of *A. pigra* in Calakmul, Mexico (Plante et al., 2014) reported that decisions on when to leave a tree were strongly affected by the satiation state of the individuals, which was defined as the amount of time spent eating earlier in the day, weighed by total foraging time. In contrast, here we considered that individuals were satiated if they spent at least one hour without feeding after their last feeding bout. Using this definition, more than 80% of the feeding bouts did not result in satiation.

Do black howler monkeys leave a feeding patch due to resource mixing?

We found that resource mixing was the most common reason for leaving a patch for unsatiated howlers. In general, howlers left productive food patches before they were depleted in order to locate a new food type that offered a different set of nutrients or secondary compounds. Other studies of patch choice and patch depletion in colobines (*C. guereza*) have suggested that resource mixing can be a major factor in primate foraging decisions (Tombak et al., 2012; Johnson et al., 2017). Moreover, feedback mechanisms and physiological factors, such as specific gut capacity and toxin thresholds, or the interacting effects of nutrients and secondary compounds (e.g., inhibition of glucose absorption by flavonoids; Karasov, 2011) provide internal signals that drive resource mixing decisions. The fact that black howler monkeys alternated feeding bouts between fruit and leaf patches, as well as alternating bouts of higher and lower protein intake, suggest that this pattern could be dictated by the need to balance nutrients.

Few studies of other vertebrates have analyzed patch choice in the wild from a resource mixing perspective. In a field experiment set out to test the "complementarity hypothesis" (i.e., daily foraging patterns characterized by a switch among different currencies, such as total energy and protein), highly frugivorous habituated curassows (*Mitu salvini* and *Crax alector*) were found to combine and alternate feeding bouts on energy-rich fruits with feeding bouts on protein-rich leaves and invertebrates, at the expenses of maximizing energy intake (Jiménez, 2004). This suggests that the observed foraging patterns were best explained by a need to meet daily macro and micronutrient requirements. In addition to achieving their protein requirements, curassows might have foraged for specific essential amino-acids present in leaves but not found in fruits, or to increase calcium intake, which is considered limiting for birds that feed on fruits and invertebrates (Levey & Martinez del Rio, 2001).

In conclusion, the analysis of feeding patch choice revealed that moving between feeding patches characterized by resources differing in their nutritional composition was the most common strategies used by black howler monkeys during their feeding bouts. Howlers rarely depleted feeding patches, and it was evident that social factors and aggressive interactions were not significant factors affecting patch choice decisions in this howler species. These results not only highlight the role of nutrient balancing in the foraging strategies of primates, but also the importance of applying adequate methodologies such as conducting all-day individual focal follows that allow to obtain reliable information on the amount of all foods eaten, the time spent in each patch, and the sequence of patches visited in a day.

Authors' Note

References

Aristizabal, J. F., Negrete-Yankelevich, S., Macías-Ordóñez, R., Chapman, C. A., & Serio-Silva, J. C. (2019). Spatial aggregation of fruits explains food selection in a Neotropical primate (*Alouatta pigra*). Scientific Reports, 9, 19452. doi:10.1038/s41598-019-55932-y

Bicca-Marques, J. C., & Garber, P. A. (2005). Use of social and ecological information in tamarin foraging decisions. International Journal of Primatology, 26(6), 1321-1344. doi:10.1007/s10764-005-8855-9

Busia, L., Schaffner, C. M., Rothman, J. M., & Aureli, F. (2016). Do fruit nutrients affect subgrouping patterns in wild spider monkeys (*Ateles geoffroyi*)? International Journal of Primatology, 37, 738-751. doi:10.1007/s10764-016-9935-8

Chapman, C. (1988). Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. Behaviour, 105(1-2), 99-116. doi:10.1163/156853988X00467

Chapman, C. A., & Chapman, L. J. (2000a). Determinants of group size in primates: The importance of travel costs. In S. Boinski & P. A. Garber (Eds.), On The Move. How and Why Animals Travel in Groups. Chicago, IL: University of Chicago Press.

Chapman, C. A., & Chapman, L. J. (2000b). Constraints on group size in redtail monkeys and red colobus: Testing the generality of the ecological constraints mod-

el. International Journal of Primatology, 21, 565-585. doi:10.1023/A:1005557002854

Charnov, E. L. (1976). Optimal foraging: the marginal value theorem. Theoretical Population Biology, 9, 129-136. doi:10.1016/0040-5809(76)90040-X

Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2006). Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. In G. Hohmann, M. Robbins & C. Boesch (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge, UK: Cambridge University Press.

Di Bitetti, M., & Janson, C. (2001). Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Animal Behavior, 62, 47-56. doi:10.1006/anbe.2000.1730

Erlenbach, J. A., Rode, K. D., Raubenheimer, D., & Robbins, C. T. (2014). Macronutrient optimization and energy maximization determine diets of brown bears. Journal of Mammalogy, 95, 160-068. doi:10.1644/13-MAMM-A-161

Felton, A. M., Felton, A., Lindenmayer, D. B., & Foley, W.J. (2009a). Nutritional goals of wild primates. Functional Ecology, 23, 70-78. doi:10.1111/j.1365-2435.2008.01526.x

Felton, A. M., Felton, A., Raubenheimer, D., Simpson, S. J., Foley, W. J., Wood, J. T., Wallis, I., & Lindenmayer, D. B. (2009b). Protein content of diets dictates the daily energy intake of a free-ranging primate. Behavioral Ecology, 20, 685-690. doi:10.1093/beheco/arp021

Felton, A. M., Felton, A., Wood, J. T., Foley, W. J., Raubenheimer, D., Wallis, I. R., & Lindenmayer, D. B. (2009c). Nutritional ecology of *Ateles chamek* in lowland Bolivia: How macronutrient balancing influences food choices. International Journal of Primatology, 30, 675-696. doi:10.1007/s10764-009-9367-9

Garber, P. A. (2000). The ecology of group movement: Evidence for the use of spatial, temporal, and social information in some primate foragers. In S. Boinski, & P. A. Garber (Eds.), On the Move: How and Why Animals Travel in Group. Chicago, IL: University of Chicago Press.

Garber, P. A., & Kowalewski, M. M. (2011). Collective action and male affiliation in howler monkeys (*Alouatta caraya*). In R.W. Sussman & C.R. Cloninger (Eds.), Origins of Altruism and Cooperation. New York, NY: Springer.

Garber, P. A., Bicca-Marques, J. C., & Azevedo Lopes, M. A. O. (2009). Primate Cognition: Integrating social and ecological information in decision-making. In P.A. Garber, A. Estrada, J. C. Bicca-Marques, E. Heymann & K. B. Strier, (Eds.), South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation. New York, NY: Springer.

Grether, G. F., Palombit, R. A., & Rodman, P. S. (1992). Gibbon foraging decisions and the marginal value model. International Journal of Primatology, 13, 1-17. doi:10.1007/BF02547724

Hailey, A., Chidavaenzi, R., & Loveridge, J. (1998). Diet mixing in the omnivorous tortoise *Kinixys spekii*. Functional Ecology, 12, 373-385. doi:10.1046/j.1365-2435.1998.00203.x

Harrison, M. J. S. (1984). Optimal foraging strategies in the diet of the green monkey, *Cercopithecus sabaeus*, at Mount Assirik, Senegal. International Journal of Primatology, 5, 435-471. doi:10.1007/BF02692269

Houston, A.I., Higginson, A.D., & McNamara, J.M. (2011). Optimal foraging for multiple nutrients in an unpredictable environment. Ecology Letters, 14, 1101-1107. doi:10.1111/j.1461-0248.2011.01678.x

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behavioral Ecology, 2, 143-155. doi:10.1093/beheco/2.2.143

Isbell, L. A. (2012). Re-evaluating the Ecological Constraints model with red colobus monkeys (*Procolobus rufomitratus tephrosceles*). Behaviour, 149, 493-529. doi:10.1163/156853912X641748

Janson, C. H., & van Schaik, C. P. (1988). Recognizing the many faces of primate food competition - methods. Behaviour, 105, 165-186. doi:10.1163/156853988X00502

Jiménez, I. (2004). Understanding vertebrate frugivores through foraging theory: patch use, diet composition and the abundance of curassow (Aves: Cracidae). PhD dissertation. St. Louis, MO: University of Missouri.

Johnson, C. A., Raubenheimer, D., Chapman, C. A., Tombak, K. J., Reid, A. J., & Rothman, J. M. (2017). Macronutrient balancing affects patch departure by guerezas (*Colobus guereza*). American Journal of Primatology, 79, 1-9. doi:10.1002/ajp.22495

Karasov, W. H. (2011). Digestive physiology: a view from molecules to ecosystem. American Journal of Physiology – Regulatory, Integrative and Comparative Physiology, 301, R276-R284. doi:10.1152/ajpregu.00600.2010

Kazahari, N., & Agetsuma, N. (2008). Social factors enhancing foraging success of a wild group of Japanese macaques (*Macaca fuscata*) in a patchy food environment. Behaviour, 145, 843-860. doi:10.1163/156853908783929188

Kazahari, N., Tsuji, Y., & Agetsuma, N. (2013). The relationships between feeding-group size and feeding rate vary from positive to negative with characteristics of food items in wild Japanese macaques (*Macaca fuscata*). Behaviour, 150, 175-197. doi:10.1163/1568539X-00003044

Kelaita, M., Dias, P. A. D., Aguilar-Cucurachi, M. S., Canales-Espinosa, D., & Cortes-Ortiz, L. (2011). Impact of intrasexual selection on sexual dimorphism and testes size in the mexican howler monkeys *Alouatta palliata* and *A. pigra*. American Journal of Physical Anthropology, 146, 179-187. doi:10.1002/ajpa.21559

King, A. J., Isaac, N. J. B., & Cowlishaw, G. (2009). Ecological, social, and reproductive factors shape produc-

er-scrounger dynamics in baboons. Behavioral Ecology, 20, 1039-1049. doi:10.1093/beheco/arp095

Koenig, A. (2000). Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). Behavioral Ecology Sociobiology, 48, 93-109. doi:10.1007/s002650000198

Kowalewski, M. M. (2007). Patterns of affiliation and co-operation in howler monkeys: an alternative model to explain social organization in non-human primates. PhD dissertation. Urbana, IL: University of Illinois.

Leighton, M. (1993). Modeling dietary selectivity by Bornean orangutans - evidence for integration of multiple criteria in fruit selection. International Journal of Primatology, 14, 257-313. doi:10.1007/BF02192635

Leighton, M., & Leighton, D. R. (1982). The relationship of size of feeding aggregate to size of food patch: howler monkeys (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. Biotropica, 14, 81-90. doi:10.2307/2387735

Levey, D. J., & Martinez del Rio, C. (2001). It takes guts (and more) to eat fruit: Lessons from avian nutritional ecology. Auk, 118, 819-831. doi:10.2307/4089834

Marshall, H. H., Carter, A. J., Coulson, T., Rowcliffe, J. M., Cowlishaw, G. (2012). Exploring foraging decisions in a social primate using discrete-choice models. American Naturalist, 180, 481-495. doi:10.1086/667587

Martin, P., & Bateson, P. (2007). Measuring Behaviour. an Introductory Guide. Cambridge, UK: Cambridge University Press.

Milton, K. (1980). The Foraging Strategy of Howler Monkeys: A Study in Primate Economics. New York: Columbia University Press.

Peres, C. A. (1996). Food patch structure and plant resource partitioning in interspecific associations of Amazonian tamarins. International Journal of Primatology, 17, 695-723. doi:10.1007/BF02735261

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2019). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-143, https://CRAN.R-project.org/package=nlme.

Plante, S., Colchero, F., & Calmé, S. (2014). Foraging strategy of a Neotropical primate: how intrinsic and extrinsic factors influence destination and residence time. Journal of Animal Ecology, 83, 116-125. doi: 10.1111/1365-2656.12119

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Righini, N., Garber, P. A., & Rothman, J. M. (2017). The effects of plant nutritional chemistry on food selection of Mexican black howler monkeys (*Alouatta pigra*): the role of lipids. American Journal of Primatology, 79, e22524. doi:10.1002/ajp.22524

Roberts, M. T., Bermingham, E. N., Cave, N. J., Young, W., McKenzie, C. M., & Thomas, D. G. (2018). Macronutrient intake of dogs, self-selecting diets varying in composition offered ad libitum. Journal of Animal Physiology and Animal Nutrition,102, 568-575. doi:10.1111/jpn.12794

Rothman, J. M., Chapman, C. A., & Pell, A. N. (2008). Fiber-bound nitrogen in gorilla diets: Implications for estimating dietary protein intake of primates. American Journal of Primatology, 70, 690-694. doi:10.1002/ajp.20540

Rothman, J. M., Chapman, C. A., & Van Soest, P. J. (2012). Methods in Primate Nutritional Ecology: A User's Guide. International Journal of Primatology, 33, 542-566. doi:10.1007/s10764-011-9568-x

Simpson, S. J., & Raubenheimer, D. (2012). The Nature of Nutrition: A Unifying Framework from Animal Adaptation to Human Obesity. Princeton: Princeton University Press.

Snaith, T. V., & Chapman, C. A. (2005). Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Piliocolobus tephrosceles*). Behavioral Ecology and Sociobiology, 59, 185-190. doi:10.1007/s00265-005-0023-x

Snaith, T. V., & Chapman, C. A. (2007). Primate group size and interpreting sociolecological models: Do folivores really play by different rules? Evolutionary Anthropology, 16, 94-106. doi:10.1002/evan.20132

Snaith, T. V., & Chapman, C. A. (2008). Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. Behavioral Ecology, 19, 1289-1296. doi:10.1093/beheco/arn076

StatSoft, Inc. (2011). STATISTICA. Data Analysis Software System.

Stephens, D. W, & Krebs, J. R. (1986). Foraging Theory. Princeton, NJ: Princeton University Press.

Stephens, D. W., Brown, J. S., & Ydenberg, R. C. (2007). Foraging: Behavior and Ecology. Chicago: University of Chicago Press.

Tombak, K. J., Reid, A. J., Chapman, C. A., Rothman, J. M., Johnson, C. A., & Reyna-Hurtado, R. 2012. Patch depletion behavior differs between sympatric folivorous primates. Primates, 53, 57-64. doi:10.1007/s10329-011-0274-2

Tujague, M. P., & Lahitte, H. B. (2013). Secuencias de forrajeo en monos capuchinos en cautiverio: Aprendizaje y memoria en contexto de grupo. Revista Mexicana de Análisis de la Conducta, 39, 39-55. doi:10.5514/rmac.v39.i3.63926

Tujague, M. P., Bacigalupe, M. Á., Lahitte, H. B., & Janson, C. (2016). Memoria espacial en monos capuchinos de Argentina: un estudio observacional en vida silvestre. Revista Argentina de Antropología Biológica, 18, 1-13. doi:10.17139/raab.2016.0018.01.01

van Hooff, J., & van Schaik, C. (1992). Cooperation in competition: the ecology of primate bonds. In A. H. Harcourt & F. B. M. de Waal (Eds.), Coalitions and Alliances in

Humans and Other Animals. Oxford: Oxford Science Publications.

Wang, E., & Milton, K. (2003). Intragroup social relationships of male *Alouatta palliata* on Barro Colorado Island, Republic of Panama. International Journal of Primatology, 24, 1227-1243. doi:10.1023/B:IJOP.0000005989.29238.ce

Ydenberg, R. C., Brown, J. S., & Stephens, D. W. (2007). Foraging: an overview. In D. W. Stephens, J. S. Brown & R. C. Ydenberg (Eds.), Foraging: Behavior and Ecology. Chicago: University of Chicago Press.

Zuur, A., Ieno, E., & Meester,s E. (2009). A Beginner's Guide to R. New York: Springer. 218 p.